J. HYM. RES.
Vol. 15(2), 2006, pp. 270–276

The Genus *Allotilla* Schuster (Hymenoptera: Mutillidae): Phylogenetic Analysis of its Relationships, First Description of the Female and New Distribution Records

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Abstract.—The morphological characteristics of the monotypic genus *Allotilla* Schuster are discussed; new distribution records and a morphology-based phylogenetic analysis are presented, clarifying possible relationships with other sphaeropthalmine genera. Females of the genus are described and illustrated for the first time; male genitalia are illustrated.

Until now, *Allotilla gibbosa* Schuster, 1949 was known only from the holotype male from Cordoba, Argentina. In a list of Mutillidae from Argentina, Fritz (1998) included Buenos Aires as an additional collection locality for this species, without providing any additional information such as the number of specimens examined, their sex, or the depository. We must consider the Buenos Aires record not to be valid because it is incomplete and because we have been unable to locate any of Fritz's *Allotilla* specimens in his reference collections at the AMNH, New York (to which they were sold by his widow after his death) or at the Museo de Ciencias Naturales "B. Rivadavia," Buenos Aires (Roig-Alsina, pers. comm.).

The female of the Neotropical, monotypic genus *Allotilla* is described and illustrated for the first time; new distribution records and a morphology-based phylogenetic analysis are presented.

MATERIALS AND METHODS

We follow Brothers (1999) for the subfamily classification of the Mutillidae. For SEM examination we used a JEOL model JSM 5600. The *Allotilla gibbosa* specimens examined are deposited in the following institutions: American Museum of Natural History, New York (AMNH); Museum of Comparative Zoology, Harvard University , Cambridge (MCZ); Museo de Invertebrados G. B. Fairchild, Universidad de Panama (MIUP); D. J. Brothers's personal collection, University of KwaZulu-Natal, South Africa (DJBC); and Institut Royal des Sciencies Naturelles de Belgique (ISNB).

RESULTS

Allotilla Schuster

Allotilla Schuster 1949: 89–93. Type species: *Allotilla gibbosa* Schuster, 1949, by original designation and monotypy.

Generic characters of female.—Body covered with simple setae only. **Head**: almost round, narrower than mesosoma; eye small, nearly circular and flat (Fig. 3); genal carina absent; scrobal carina absent; antenna 12-segmented; antennal tubercle strongly projecting, with low lamellate ridge on anteromedial surface (Fig. 3); mandible slender, with preapical tooth nearly obsolete or totally absent (Fig. 3); mandible evenly arcuate on ventral margin, without tooth or constriction; proboscidal fossa with carina nearly reaching inner mandibular base; hypostoma without tooth or tubercle; maxillary palp 6-seg-

mented; labial palp 4-segmented, the second segment almost as long as wide. **Mesosoma**: broader than long, pyriform (Fig. 4); dorsum strongly convex, without transverse carina along posterior margin of pronotum or lateral carina; dorso-lateral margins without spines; scutellar scale absent; mesopleuron swollen; leg with apex of tarsus simple, not produced above claws. **Metasoma**: first metasomal tergum not constricted posteriorly, sessile with tergum 2 (Fig. 5); tergum II evenly convex, without rows of longitudinal carinae; tergum II with felt lines; sternum II without felt lines; tergum VI with surface totally sculptured and evenly merging with rest of tergum, pygidial area poorly defined by postero-lateral carina, only visible under high magnification (>30×) (Fig. 6).

Allotilla gibbosa Schuster, 1949
(Figs 3–8)

Allotilla gibbosa Schuster, 1949: 93–95, Holotype male, Argentina: Cordoba, col. W. M. Davis, Harvard University, MCZ, type 30516, examined.

Description of female.—Integumental color: head, mesosoma, all metasomal sterna, terga I, III and IV, reddish brown; antennae and legs yellow-red; mandible reddish brown except apical third blackish; tergum II reddish brown except posteriorly with two lateral, transverse, black spots interrupted medially; terga V and VI black. **Head**: vertex and gena with sparse, medium-sized punctures one or more diameters apart (Fig. 3); punctures of frons denser, less than one diameter apart; vertex and frons with long, sparse, erect and semi-erect, dark setae; gena, clypeus laterally and hypostoma with long, sparse, pale setae. **Mesosoma**: pronotum and mesonotum with punctures as on vertex (Fig. 4); metanotum with transverse reticulate band (Fig. 4); dorsum of propodeum mostly densely micropunctate-rugose (Fig. 4) except a narrow impunctate area near metanotum; mesopleuron with dense, medium-sized punctures, except for mostly impunctate anterior area near lateral area of pronotum; metapleura and lateral area of propodeum impunctate, smooth; setation of pronotum, mesonotum and metanotum similar to that of vertex; mesopleura and dorsum of propodeum with pale setae; metapleura and lateral area of propodeum glabrous. **Metasoma**: terga I and II with small, dense punctures, sparser in apical areas (Fig. 5); terga III and IV with small, sparse punctures; tergum V mostly smooth, except basal lateral area with a few punctures; tergum VI with scale-like surface sculpture basally, scales diminishing in size toward apex, gradually turning into granules (Fig. 6); sterna I and VI smooth; sterna II and III with small, somewhat sparse punctures; sterna IV and V mostly smooth, except apex with small, dense punctures; tergum I mostly with pale setae, a few dark setae at apex; tergum II with dark setae, except lateral area and apex with pale setae; terga III and IV mostly with pale setae; tergum V mostly glabrous, with a few pale and dark setae laterally; tergum VI glabrous; sterna I to V with pale setae; sternum VI glabrous.

Additional male characters.—The external male genitalia and the penis valve (Figs 7–8) are illustrated here for the first time (paramere, cuspis and digitus were described previously but not illustrated). The volsella has distinctive long setae on the cuspis apex (Fig. 7). The penis valve has a subapical tooth, more distant from the apical tooth than in males of *Protophotopsis* (see Figs 11–14, Cambra and Quintero 1997).

Material examined (56 males, 5 females).—All males were captured with Malaise traps (B. Garcete coll.) and females with pitfall traps (T. Delsinne coll.). PARAGUAY: **Boquerón** Department: Parque Nacional Teniente Enciso, Administración, 239 m (21° 12′ S, 61° 39′ W) 16–19 Sep 2003, 20 males [MIUP, DJBC]; same loc., 20–24 Mar 2004, 6 males [MIUP]; same loc., 23–26 Sep 2004, 3 males [MIUP]; Siracua, 275 m (21° 02′ S, 61° 45′ W) 20–22 Sep 2003, 21 males [MIUP, MCZ, AMNH, ISNB, DJBC]; Estancia Maria

Vicenta, 235–244 m (20°55′ S, 61°23′ W) 26–30 Sep 2004, 5 males [MIUP]; TransChaco, Mister Long, (20°35′ S, 62°02′ W), 17 Sep 2003, 1 female [MIUP]; Parque Nacional Teniente Enciso, TransChaco, 23–25 Sep 2004, 3 females [MIUP, ISBN, DJBC]; same data but 24–25 Sep 2003, 1 female [MCZ]. **Presidente Hayes** Department: Reserva Tinfunke, La Verde, 146 m (23°56′ S, 69°29′ W) 29 Nov–1 Dec 2003, 1 male [MIUP].

Variations.—Female frons dark reddish brown to black; tergum IV varying from totally reddish brown to black or the lateral areas black with reddish brown in the middle. Males from Paraguay are identical to the holotype, except that the propodeal lateral area is rugose on the holotype, but punctate with smooth areas to rugose-punctate or totally rugose in specimens from Paraguay. We consider this variation to be size-related: male rugosity increases with body length. In addition, larger males have the notauli nearly obsolete (same as the holotype), but notauli are absent in smaller males. Total length, females: 3.5–5 mm; males: 4–7 mm.

Distribution.—Paraguay and Argentina. *Allotilla gibbosa* was previously known only from the holotype from Cordoba, Argentina.

PHYLOGENETIC ANALYSIS

Taxa.—To test the subtribal position of *Allotilla* (currently included in the subtribe Pseudomethocina, Brothers 1975), and to recognize its phylogenetic affinities, we selected as the outgroup the following two genera: *Timulla* (Mutillini) and *Dasylabris* (Dasylabrini, genus not present in America); as ingroup taxa, we selected the following 17 Sphaeropthalmini genera, with mainly South American distributions and fully winged males: ten Pseudomethocina (*Euspinolia, Tallium, Atillum, Calomutilla, Horcomutilla, Pseudomethoca, Hoplocrates, Pappognatha, Hoplomutilla* and *Allotilla*), females with head transversely subquadrate, broader than the mesosoma, genal carina present (except *Euspinolia* and *Tallium*), first metasomal segment sessile, evenly merging with second; and seven Sphaeropthalmina (*Nanotopsis, Protophotopsis, Reedomutilla, Scaptodactyla, Limaytilla, Suareztilla and Limaytilla*), females with head nearly round, narrower than the mesosoma, and genal carina absent.

Characters.—Twenty-three binary and multistate characters of adult male (M) and female (F) external morphology and male genitalia were coded for analysis; all were treated as unweighted and unordered. No autapomorphies were used. The character matrix used is given in Table 1. The following characters were employed for cladistic analysis:

Head:

1. Head shape (F): 0—small, almost round, not broader than mesosoma; 1—transversely subquadrate, large, distinctly broader than mesosoma.
2. Head (M, F): 0—without large conical projection ventrally; 1—with large conical projection ventrally.
3. Scrobal carina (F): 0—present; 1—absent.
4. Genal carina (F):—absent; 1—present.
5. Mandible basal ventral margin (M, F): 0 - with constriction; 1—with broad lamellate projection; 2—almost straight.
6. Antennal tubercle (F): 0 - without lamellate projection; 1—with lamellate projection on anteromedial surface.
7. Antenna (F): 0–12-segmented; 1–13-segmented.
8. Ocelli (M): 0—small (diurnally active); 1—large (nocturnally active).

Mesosoma:

1. Dorsum of mesosoma (F): 0—longer than broad, sometimes as broad as or slightly broader than long; 1—distinctly broader than long.
2. Shape of mesosoma (F): 0—subrectangular; 1—violin- shaped, strongly constricted at the propodeal spiracles; 2—pyriform.
3. Axilla of mesonotum (M): 0—not expanded; 1—expanded posterolaterally as a rectangular or acute protruberance.
4. Scutellar scale (F): 0—present; 1—absent.
5. Notauli (M): 0—present; 1—absent.

Table 1. Data matrix for the 23 characters used in the phylogenetic analysis

Taxon	Characters																						
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
*Timulla**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Dasylabris**	0	0	1	0	0	0	0	0	0	2	1	0	1	2	0	0	1	2	0	0	0	0	0
Euspinolia	1	0	1	0	2	1	0	0	0	0	0	1	0	2	0	1	0	1	0	0	1	0	0
Tallium	1	0	1	0	-	-	0	0	0	0	0	0	0	2	0	1	0	1	0	0	1	-	0
Allotilla	0	0,	1	0	2	1	0	0	1	2	0	1	-	0	0	1	0	1	0	0	1	0	0
Nanotopsis	0	0	1	0	2	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0
Protophotopsis	0	0	1	0	2	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0
Scaptodactyla	0	0	1	0	2	1	0	1	1	2	0	1	0	0	0	1	0	2	0	0	0	1	0
Atillum	1	1	0	1	-	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0
Hoplocrates	1	1	0	1	1	0	1	0	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0
Hoplomutilla	1	0	0	1	2	0	0	0	0	1	0	1	1	1	1	1	1	0	-	0	0	0	0
Pappognatha	1	0	0	1	1	0	0	0	0	2	0	1	1	1	1	1	1	1	1	1	0	0	0
*Pseudomethoca**	1	0	0	1	2	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0
Calomutilla	1	0	0	1	2	0	0	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0
Horcomutilla	1	0	-	1	2	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0
Xystromutilla	0	0	1	0	2	0	0	0	0	2	0	1	0	0	0	1	1	2	1	1	1	1	0
Reedomutilla	0	0	1	0	2	0	0	0	0	2	1	1	1	0	0	1	1	2	0	0	0	0	1
Suareztilla	0	0	0	0	2	0	0	0	0	2	1	1	1	2	0	1	1	2	0	0	0	0	1
Limaytilla	0	0	1	0	0	1	0	1	1	2	0	1	0	0	0	1	0	2	0	0	1	1	0

(- = not applicable or with intragroup variation)
*Only the type species examined: *Timulla dubitata* (Smith), *Pseudomethoca frigida* (Smith) and *Dasylabris* (*Dasylabris*) *maura* (Pallas).

6. Mesosternum posterior margin (F): 0—with short triangular or spiniform process; 1—with large truncate laminate process between and over inner margins of posterior coxae; 2—obsolete spiniform or triangular process.
7. Tarsomere 5 (M, F): 0—apex not produced above base of claws; 1—apex produced above base of claws, forming lamellate plate.
8. Pterostigma (M): 0—slightly sclerotized, membranous or absent; 1—heavily sclerotized.

Metasoma:

1. Tergum I (F): 0—broad, sessile with second apically; 1—nodose, disciform or petiolate, not sessile with second.
2. Tergum I (M): 0—broad, sessile with second apically; 1—subsessile-campanulate at apex; 2—nodose or petiolate with distinct lateral constrictions apically.
3. Tergum VI (F): 0—defined by lateral carinae; 1—not defined by lateral carinae.
4. Tergum VI (F): 0—mostly flattened, broad and generally totally sculptured (punctate, rugose, granulate or striate); 1—more convex, not broad, with a medial smooth area or entirely smooth.
5. Felt line on sternum II, lateral margin (M): 0—absent; 1—present.
6. Setae, 40× (M, F): 0—only simple; 1—both simple and plumose.
7. Parameres (M): 0—scarcely recurved apically or almost straight; 1—apex sharply and strongly recurved apically.

Characters of male genitalia not examined in all genera but considered potentially useful in a future phylogenetic analysis of the Sphaeropthalminae are: shape of cuspis, digitus and penis valve. The following characters were examined but not used because these characters need a more detailed study to determine if intragroup variation modifies them: length of antenna; eye size; sculpture of head; number of teeth on apex of mandibles; propodeum teeth; length of pterostigma and second submarginal cell.

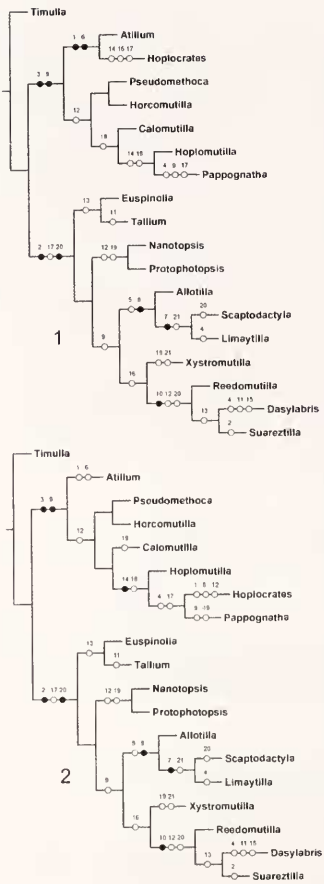
The following characters were examined but not used because they probably repre-

sent autapomorphies in the present analysis: posterolateral tubercles on vertex, present in some females of *Dasymutilla*, *Traumatomutilla* and *Cephalomutilla*; mandibles covered with dense, short pubescence, an autapomorphy of *Pappognatha*; humeral angle of pronotum produced as a hook-like tooth, an autapomorphy of *Gurisita* females (males unknown); posterior coxa with tooth apically on inner margin, an autapomorphy of *Vianatilla* females; tibia 2 with one apical spur, an autapomorphy of *Acanthophotopsis* males; males apterous or brachypterous, *Morsyma* (apterous), *Myrmilloides* and *Stethophotopsis* (brachypterous), *Dasymutilla* (rarely brachypterous); tergum II with arcuate transverse band of dense, curled setae and slight integumental ridge at anterior margin of band, in most *Dimorphomutilla* females; female with felt line on sternum II, autapomorphy of *Patquiatilla*; sternum II with anteromedian seta-filled pit, in some males of *Dasymutilla* and *Traumatomutilla*; tegula elongated to or beyond the level of transscutal articulation, autapomorphy for *Timulla* males; eye inner margin deeply and abruptly notched, autapomorphy for *Timulla* males.

A heuristic search of trees derived from parsimony analysis was carried out using NONA version 2.0 using WinClada version 1.00.08 (Nixon 2002), resulting in four cladograms. We preferred two of these minimal-length cladograms (Figs 1–2), see Results and Discussion. The following options were used: maximum trees to keep = 1000; number of replications (mult*N) = 1000; starting trees per rep (hold/) = 100; random seed = 1000; unconstrained search; search strategy of multiple TBR + TBR (mult* max*).

RESULTS AND DISCUSSION

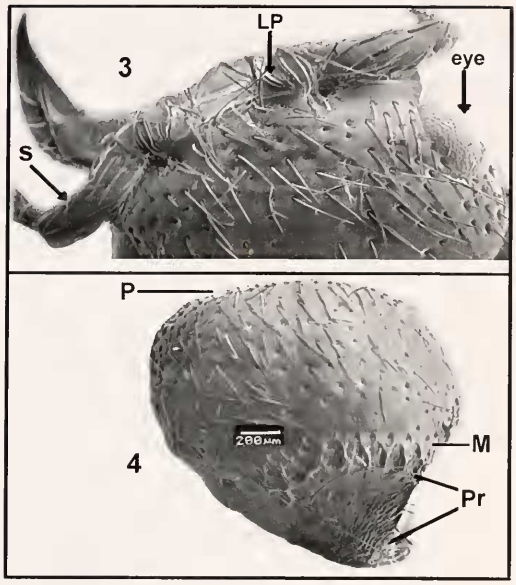
The female of *Allotilla gibbosa* was recognized based on morphological similarities to the known male, mainly the distinctive and peculiar inflation and broadening of



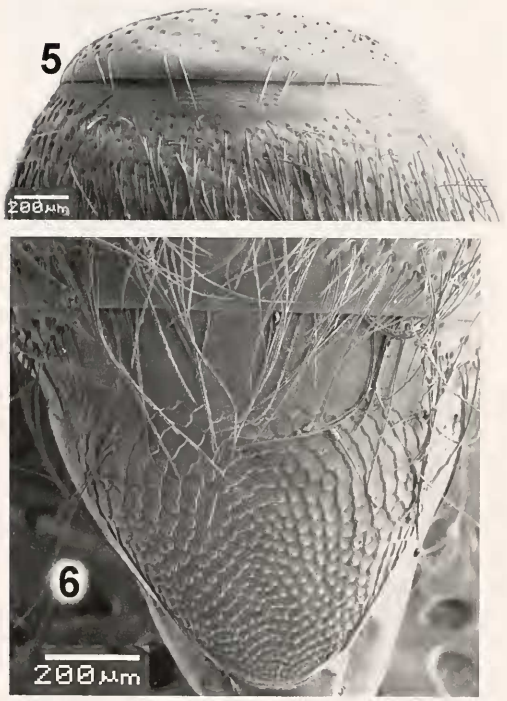
Figs 1–2. Preferred minimum-length cladograms of four trees derived from heuristic analysis of the character data presented in Table 1 using ratchet (WINCLADA) and mult* (NONA). Tree length = 62; consistency index = 0.43; retention index = 0.66. Synapomorphies are show by the black circles.

the mesosoma, and because these were the only female and male Sphaeropthalminae collected from the same geographic area, Paraguay's Chaco, that we recognized as belonging to a genus whose female was not known.

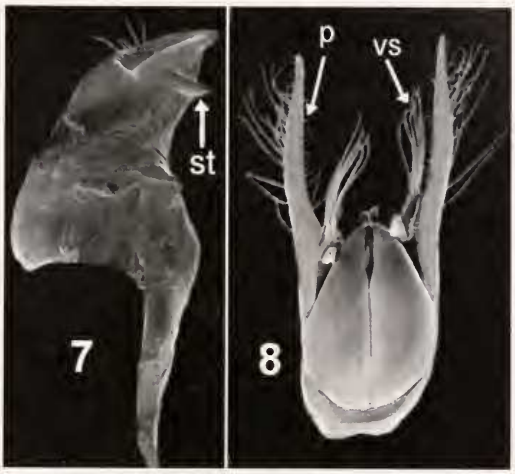
The relationships between American mutillid genera (none is known to be present outside of America, except for *Timulla*) and those of Africa and Australia are almost totally unknown, although different but closely related genera are involved. Vicariant biogeographical hypotheses and their common ancestral geo-



Figs 3–4. *Allotilla gibbosa*, female. 3. Head, dorsal view. 4. Mesosoma, postero-dorsal view. Abreviations: LP = lamellate projection of antennal tubercle, M = metanotum, P = pronotum, Pr = propodeum, S = scape.



Figs 5–6. *Allotilla gibbosa*, female metasoma, dorsal view. 5. Tergum 1 and basal part of tergum 2. 6. Tergum 6.



Figs 7–8. *Allotilla gibbosa*, male genitalia. 7. Parameres dorsal view. 8. Penis valve, lateral view. Abbreviations: P = paramere; ST = subapical tooth; VS = volsellar setae.

graphic areas suggest close evolutionary relationships with South American genera. Some genera widely distributed in the Americas, such as *Sphaeropthalma* and *Traumatomutilla*, cannot be included in the present cladistic analysis because they are as yet poorly defined.

The heuristic analysis resulted in four cladograms, the two preferred minimal-length cladograms (Figs 1–2) postulate a sister relationship of *Allotilla* with *Scaptodactyla* and *Limaytilla*. The other two cladograms postulate a less parsimonious, complex relationship for the selected South Amerian taxa and, following Occam's razor, were not accepted: *Allotilla* + [(*Scaptodactyla* + *Limaytilla*) + (((*Xystromutilla* + ((*Reedomutilla* + (*Dasylabris* + *Suareztilla*)))].

These preliminary cladograms suggest than *Allotilla* is more closely related to genera in the subtribe Sphaeropthalmina than to those in the Pseudomethocina. At present, we do not know of any unique morphological characters to separate these two subtribes.

The biology of *Allotilla gibbosa* is unknown, but the black integument, moderately sized eyes, and very small ocelli of the males suggest that they are diurnal. The following morphological characters of

Allotilla females indicate that they spend most of their lives underground: small, flattened eyes, relatively short legs with a fore tarsal rake (used to excavate soil), and a mostly reddish-brown integument. Extensive visual samplings carried out during daylight hours in Teniente Enciso National Park did not yield any *Allotilla* females from the ground or on the sparse vegetation; females were collected only with pitfall traps. These capture data lend support to the postulated underground, burrowing habits of the females. Probably they parasitize small, underground-nesting aculeates. Females of the here-recognized closely related sphaeropthalmine genera, *Scaptodactyla* and *Linnaytilla*, sister genera to *Allotilla*, have a similar morphological habitus, suggesting that they have similar hypogeal lives and burrowing activities.

A morphology-based phylogenetic analysis of 18 mostly South American mutillid genera and one from outside America (*Dasylabris*) permits us to construct a hypothetical scenario of biogeographic divergences. The vicariant event that divided the population of the common ancestor of the taxa presented in Table 1 was the uplifting of the Andean high mountain range. This uplifting event was followed by ecological divergence of the two Andean regions: the elongated West costal region, draining into the Pacific Ocean, isolated from a more extensive and ecologically diverse Eastern region. The ancestor population of the present-day *Euspinolia*, an almost exclusively Chilean and Peruvian taxon, was isolated on the Pacific Andes slopes. The common ancestor of both *Tallium* and *Linnaytilla* + *Scaptodactyla* + *Allotilla* was relegated to the region east of the Andes. The climatic and vegetational changes brought about by the Andean uplift, particularly the desertification of the Chaco region, was the driving selective force that caused the diversification and evolutionary split between *Tallium* and the sister genera of *Allotilla* + *Scaptodactyla* + *Linnaytilla*.

Spichiger et al. (2004), investigating the geographical zonation in South America of 32 common tree species encountered in Paraguay, found that the xeromorphic forests of the Chaco area act as an edaphic barrier to many species that are centered in northern Argentina. The genus *Allotilla* is reported only from northern Argentina and Paraguay.

If additional sphaeropthalmine genera eventually are included in the data matrix presented here, the larger data matrix might provide a better resolution in the phylogenetic analysis.

ACKNOWLEDGMENTS

Our sincere thanks to Thibaut Delsinne, ISBN, for sorting and sending us all the mutillids from his pitfall traps from Paraguay. We are grateful to Philip D. Perkins, MCZ, for the loan of the holotype of *A. gibbosa*; Bolivar R. Garcete B., Museo Nacional Historia Natural de Paraguay for collecting mutillid specimens; Annette Aiello, Smithsonian Tropical Research Institute, and Denis J. Brothers, University of KwaZulu-Natal, South Africa for reading the manuscript and for providing us with very helpful suggestions to improve its contents; Alcides Muñoz, University of Panama, for SEM work.

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